CHARACTERISTICS OF COURTSHIP AND MATING BEHAVIOUR USED AS CLASSIFICATORY CRITERIA IN EULOPHIDAE-TETRASTICHINAE (HYMENOPTERA), WITH SPECIAL REFERENCE TO THE GENUS *TETRASTICHUS* s.l.

by

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Abstract

The usefulness of behavioural characters for taxonomic work was tested in a comparative study of courtship and mating behaviour of Chalcidoidea-Tetrastichinae. In particular, species-groups of the large genus *Tetrastichus* were scrutinized. Similarities and differences are discussed. Transformations between character-states are found which seem to reflect developments in the evolution of this group of wasps. Earlier, parallel developments were traced in other families of Chalcidoidea (e.g. in Pteromalidae, Encyrtidae).

Within the Eulophidae, the subfamily Tetrastichinae represents a morphologically well-defined entity. However, the present subdivision of this taxon is unsatisfactory. The current practice (Bouček, 1977) is to distinguish 17 genera (exclusive of several poorly known Girault genera), most of which with a single or a few species. Amongst this group *Tetrastichus* stands out with well over 200 species in Europe alone (and a comparable number in North America, ignoring other areas). *Tetrastichus* is subdivided in species groups and a number of *species solae*, but the general feeling is that it does not represent a natural entity. Very probably some of the species groups should be raised to generic rank. Graham (1961) realized the necessity to split up *Aprostocetus* (= *Tetrastichus*), but he expressed as his opinion "that such subdivision will have to be based upon new combinations of characters, those hitherto employed being unreliable for generic diagnosis".

It is at this point that we venture to present a type of character not employed so far in this group. Earlier (Van den Assem & Povel (1973); Van den Assem (1974)) characteristics of courtship behaviour as taxonomic criteria were used in a few groups of Pteromalidae and we presumed that in the Tetrastichinae courtship could also offer a set of valuable characters for defining entities above the level of species.

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For various reasons the Tetrastichinae seem to represent a favourable group for a comparative study of courtship behaviour. Recently, a number of entomologists has become interested in this group and, most important, are preparing revisions of several genera of Tetrastichinae. These revisions will offer good opportunities for a comparison of arrangements of species and groups of species (and assignment of generic-status) on morphological criteria with one based on characteristics of display behaviour.

There were additional reasons for choosing the Tetrastichinae. Preliminary observations led us to suppose that in this group, and in the whole complex of Eulophidae for that matter, evolution of courtship had proceeded parallel to developments traced in other groups of Chalcidoidea, viz., Pteromalidae and Encyrtidae. *Tetrastichus* especially is extremely rich in clusters of closely related species. Comparison of displays may give an idea of processes involved in species radiation.

We thought it possible to collect a good many species within a reasonable period of time and, judging by our experience with Pteromalidae, courtship behaviour did not need complicated arrangements before it could be observed in the laboratory. As to this latter point, our expectations have not completely been realized. We have collected 39 species of *Tetrastichus* and about a dozen of *Melittobia* (a review of our *Tetrastichus* material is given in the Appendix), but some of them never courted, not even when we patiently waited for hours. It is impossible to

understand why this should be so. Presumably one or more environmental factors were amiss. For example, the males of *T. asparagi* did not court conspecific females in a bare glass vial, or only briefly, with long intervals. Adding a small quantity of dry sand made the males court immediately, and removal of the sand made them stop again. Adding sand to other non-courting species did not have the desired effect.

With some species we obtained only very few specimens and sometimes a male had died before one or more females had emerged. In yet other species males proved to be very rare or absent. Thelytoky is presumed to be the rule in those species.

CHARACTERISTICS OF COURTSHIP BEHAVIOUR SHARED BY ALL TETRASTICHINAE

A number of characteristics of the courtship display are shared by all species of Tetrastichinae. These general aspects are reviewed below. More specific properties of displays will be dealt with in the following sections.

Prior to the onset of courtship proper, the male mounts the female and takes up a courtship position on top of her. The precise placement of the male's front tarsi varies between species (on the thorax, neck, back of head, or face of the female), but the position almost never varies within a species (*T. lasiocera* was the only exception).

The position of the male's head relative to the female's changes periodically during the performance of his display, and accordingly we distinguish "high"-phase episodes and "low"-phase

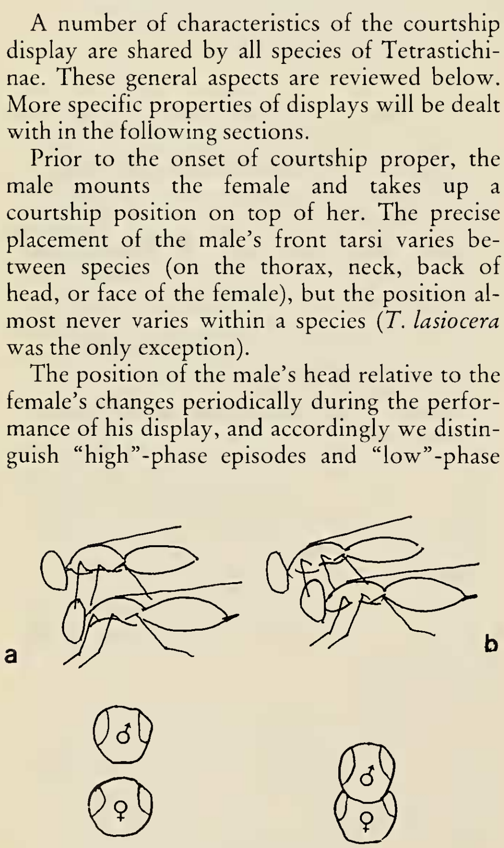


Fig. 1. Schematic representation of the positions of male relative to female during the "high"- and "low"-phase episodes; a, b, high, resp. low from aside; c, d, high, resp. low positions of heads from the front.

episodes; see fig. 1 for a schematic representation. Usually these changes are very conspicuous (except in a few species where it is less so, and only rarely high phases appear to be entirely absent). The high-phase position of the male is achieved primarily by stretching his front legs, his front tarsi remaining in the same position throughout. As a consequence his head comes further from the female's than during the low phase (when the male has bent his front legs to some extent). In the low phase a contact between heads or their appendages (antennae, mouth parts) is a frequent occurrence.

There is a second alternation, synchronous to the high-and-low one: in the low phase the male's entire body is situated more to the front (in several species rather extremely so) and in the high phase more to the rear, relative to the female. These shifts are also due to the movement of the male's legs, while his front tarsi remain in the same position.

A sequence of male courtship consists of a repetition of identical bouts of movements. In some species bouts of one type of movements alternate with bouts of another; in other species successive bouts may be separated by intervals which seem to be "rest"periods.

They can be presented schematically as follows:

low: bout → *high*: rest → *low*: bout → *high*: rest, etc.,

or,

low: bout a → *high*: bout b → *low*: bout a → *high*: bout b, etc.

In this respect the majority of *Melittobia* species are the single exception we know of: here a sequence of courtship is not confined to the mere repetition of similar elements but new elements come in underway (Van den Assem, 1975).

A courting male may move several limbs in fixed patterns. The details of the movements are specific but all species perform movements with the antennae and almost all vibrate wings. In cases where we have recorded these vibrations on tape, we obtained specific sound patterns (Van den Assem & Putters, 1980). In some genera leg movements are involved, but in *Tetrastichus* such cases seem to be rare.

When sexually receptive, the female raises her abdomen to expose the genital orifice. At the same time she lowers herself to the substrate and stretches her head to the front with the antennae pointing upwards. This posture holds for all Tetrastichinae. Females may become recep-

tive at certain points of a male's display, e.g., always at the end of a low phase. Since the male repeats similar motor patterns periodically, the onset of female receptivity cannot be predicted accurately beforehand. *Melittobia* females are exceptional again: they will indicate receptivity at only one single point, following the male's finale (Van den Assem, 1975).

Following copulation a male may either walk away from the female, or he may resume courtship from the position characteristic for the species. Post-copulatory sequences were observed in some species. The motor patterns involved in post-copulatory displays are identical to those of pre-copulatory displays; post-copulatory sequences are usually rather short.

Characteristics of courtship displays of *Tetrastichus* species groups

Within the genus *Tetrastichus* there are several morphologically recognisable species groups. With a number of such groups we were lucky enough to collect more than one species. The first question is, whether there is a greater resemblance in courtship displays between species of one species group than between species from different groups. Resemblances and differences were found indeed, and we will return to this point in the discussion. Below we give descriptions of the displays of different species groups of *Tetrastichus*. A few additional species which belong to related genera (and which happened to turn up in our collection) are also discussed. We have tried to follow a standard pattern in our descriptions, and abbreviate as much as possible to avoid repetition and save space. The groups are arranged in an alphabetical order.

a. *Tetrastichus*, group *arundinis*; species observed: *T. arundinis*, *T. gratus*, *T.* spec. 9 (fig. 2).

In general there is a distinct alternation of "high, and less frontal" and "low, and more to the front" phases. The male front tarsi are placed on the female's head, usually on her face. During the high phase the male holds his antennae in a curved position above the female's and vibrates them at a high frequency. At the onset of a low phase the male bows low, lowering his antennae and waving them in front of the female (e.g., in spec. 9; fig. 2b, c, d), or, instead, the male actually grasps the female's antennae briefly, holding his antennae in such a way that his flagellar parts point backwards and touch the female's mouth parts. At the onset of a high phase the male raises his antennae slowly. The female indicates receptivity at the end of a low phase. Copulation lasts about 5 secs. No post-copulatory courtship observed.

In *T. arundinis* males the alternation of low and high (in this species it is far more an alternation between less frontal and extremely frontal) was most pronounced; in spec. 9 it was far less pronounced. The alternation appeared completely stereotyped in *T. arundinis*, contrary to spec. 9 where the high-phase duration was variable. Vibrating the antennae above the female's antennae during the high phase was most conspicuous by far in *T. gratus*. Embracing the female's antennae during the low phase was most pronounced in *T. arundinis*, the males grasping the female's antennae from the sides with their own antennae, pushing them together, freezing in this posture for a second or so, their claval parts in contact with the female's mouth parts

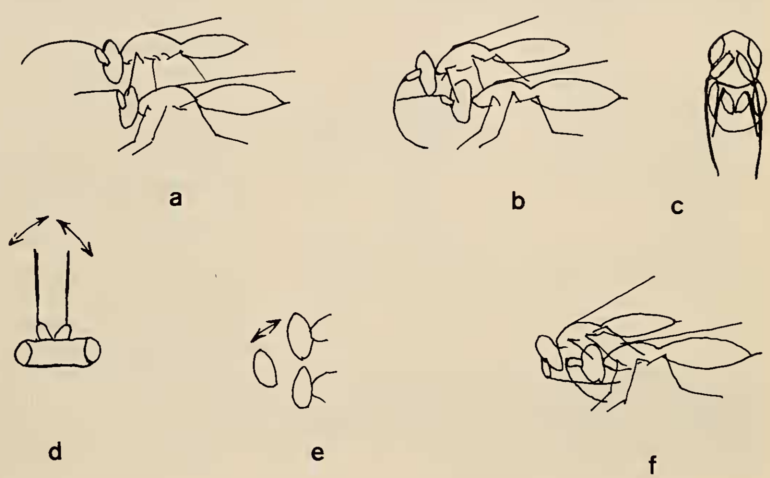
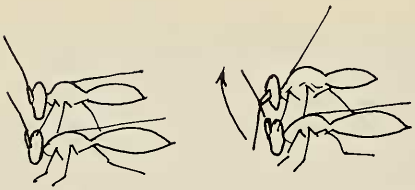


Fig. 2. *T. arundinis* group; a, high phase positions; b, low phase positions of *T.* spec. 9 from aside; c, position of male antennae of *T.* spec. 9 seen from front, and d, seen from top; e, *T. arundinis*, positions of male head in low and high phases; f, *T. arundinis*, low phase positions seen from side.



a b

Fig. 3. *T. brevinervis* group; *T. lasiocera*; a, high phase, b, low phase positions, in sideview.

(fig. 2f). Leg movements (series of drumming the front tarsi on the female's head) were observed in *T. gratus*; they did not occur in the other species.

b. *Tetrastichus*, group *brevinervis*; species observed: *T. lasiocera* (fig. 3).

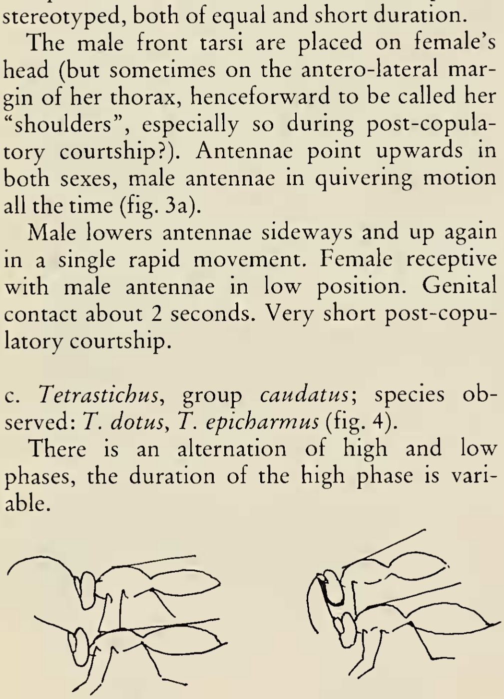
There is no clear difference between high and low positions of the male. Alternation of phases stereotyped, both of equal and short duration.

The male front tarsi are placed on female's head (but sometimes on the antero-lateral margin of her thorax, henceforward to be called her "shoulders", especially so during post-copulatory courtship?). Antennae point upwards in both sexes, male antennae in quivering motion all the time (fig. 3a).

Male lowers antennae sideways and up again in a single rapid movement. Female receptive with male antennae in low position. Genital contact about 2 seconds. Very short post-copulatory courtship.

c. *Tetrastichus*, group *caudatus*; species observed: *T. dotus*, *T. epicharmus* (fig. 4).

There is an alternation of high and low phases, the duration of the high phase is variable.



a b

Fig. 4. *T. caudatus* group; *T. epicharmus*; a, high phase positions, and b, low phase positions, in sideview.

Male front tarsi are placed on the female's "shoulders". The female's antennae point upwards throughout, the male's antennae point upwards during high phases only.

A low phase starts with the male bending slightly forward. His antennae are bent low and are in a quivering motion in front of the female's head. The male's body is rocking from side to side and his wings are vibrating. The male antennal movements are very simple, there is no raising sideways nor rubbing against or hitting on the female's antennae.

Copulation follows at the end of a low phase.

Males of *T. epicharmus* pressed their "face" against the female flagellar parts at the onset of the low phase, and their wings vibrated in very distinct pulses. During the low phase they swayed their middle legs far to the front. Such leg movements seem to be exceptional in *Tetrastichus*, this is the only species in which we observed them. Similar movements occur in all *Melittobia*. At the end of a low phase males of *T. epicharmus* quiver the antennae in front of the female's antennae; males of *T. dotus* hold the antennae alongside the female's antennae for a short moment and then resume the high-phase position.

d. *Tetrastichus*, group *daira*; species observed: *T. daira*, *T. diaphantus*, *T.* spec. 3, *T.* spec. 4 (fig. 5).

There appears to be some discrepancy between the display of *T. daira* and those of the other species. However, there are also striking similarities.

In *T. daira* alternation of phases occurs not so much between high and low but rather between more-frontal and less-frontal. The less-frontal phase is shorter than the more-frontal.

Males of *daira* place the front tarsi on the female's "shoulders". In the less-frontal phase the female's antennae point forward, as do those of the male.

At the start of the more-frontal phase the male performs series of antennal quivering (moving his antennae in between her's, while knocking them on her head) and he rocks his body from side to side (fig. 5a). At the end of the quivering episode, the female has raised her antennae (fig. 5b, c). The male raises his sideways, keeps them thus for short moment (in a position resembling that of *miser*-group species) and proceeds with series of (about three) lashing movements along the outside of the female's antennae, hitting her on or near her mouth parts (fig. 5d). These hits are accompanied by wing flicks.

Females become receptive at the end of lashing series; a receptive female's head is only

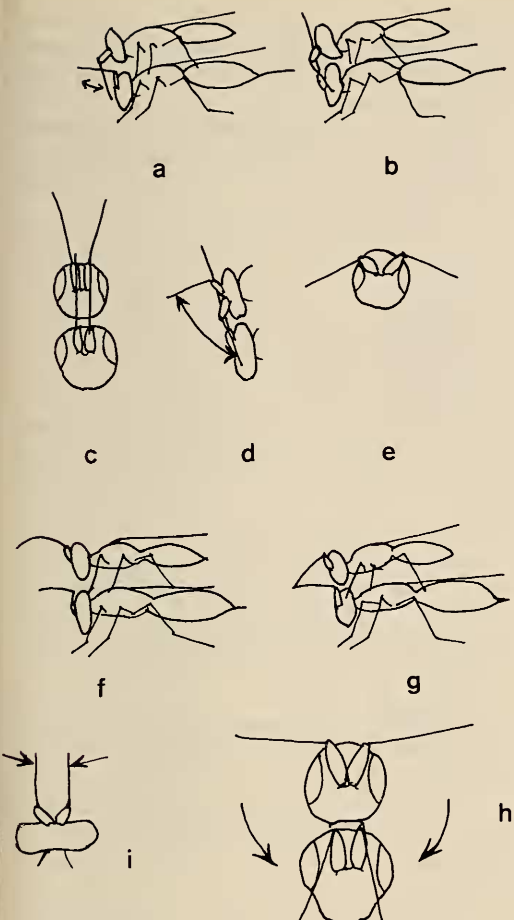


Fig. 5. *T. daira* group; a—e, *T. daira*; f—i, *T. diaphantus* c.s.; a, antennal quivering posture, and b, hitting the female's head; c, antennae raised; d, antennae hitting female's head in sideview, the arrow indicates the way of raising antennae in between hits; e, antennae raised in between hits, from front; f, g, high and low phase positions; h, antennal hits, seen from front, and i, from top.

slightly forward. Genital contact about 5—10 seconds. *T. daira* males always performed post-copulatory courtship and females showed renewed receptivity, which resulted in all of them in a succession of four copulations.

In the other *daira*-group species differences between high and low were more distinct (fig. 5f, g) than in *T. daira*. In these species male front tarsi are placed on the female's head (most extreme in *T. diaphantus* with front feet placed on her face). Female antennae never point upwards and male antennae are curved and held forward above the female's during high phase.

During the low phase male antennae follow a *daira*-like pattern. There is a quivering episode at the beginning and male antennae make rhythmical contact with the female's flagellar parts near her pedicel. His mouth parts are near her pedicel. The male's body rocks slightly from side to side. The male proceeds with raising the antennae sideways and hits the female's antennae from the outside a few times in rapid succession (fig. 5h, i). Antennal hits are accompanied by wing flicks. Males of spec. 4 drum the hind legs on the female's wing edges following antennal hits.

Female receptivity occurs during the antennal-lashing episode. Genital contact about 5 seconds. There were sequences of post-copulatory courtship.

e. *Tetrastichus*, group *evonymellae*; species observed: *T. evonymellae, T. galactopus* (fig. 6).

The alternation of high and low phases is very distinct, the high phase is of a variable duration.

Male front tarsi are placed on the female's "shoulders". Female antennae point upwards throughout. During the high phase the male's antennae are in a similar position, forming a sharp figure V, his wings standing up (fig. 6a).

At the beginning of a low phase the male lowers his head until it almost touches the female's vertex, while spreading his antennae sideways. This movement is followed by rapidly rubbing his antennae along, or knocking them against the outside of hers (fig. 6b). The female's head did not appear to be hit (movements are ex-

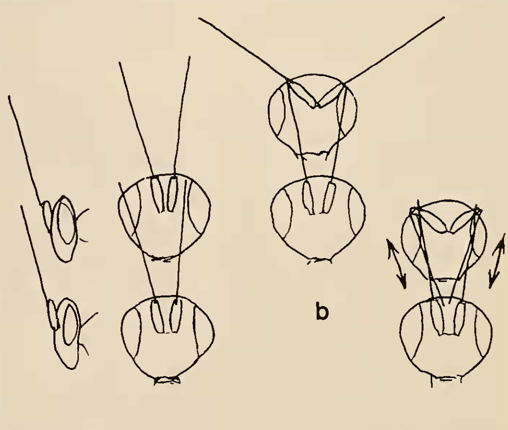


Fig. 6. *T. evonymellae* group; a, head positions and positions of the antennae during the high phase, in sideview and from front; b, and c, idem, during low phase.

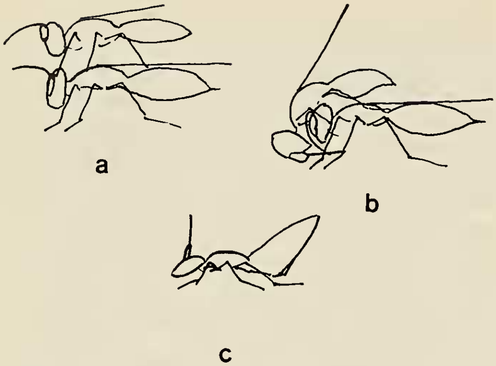


Fig. 7. *T. fulvipes* group; a, high phase, and b, low phase positions of *T. calamarius*; c, copulation posture of female.

tremely rapid) (fig. 6c). Knocks come in series of one to three, at the end of a series the male resumes the high-phase position.

The female becomes receptive during antennal knocking, she lowers the frontal part of her body, stretching her head to the front, sometimes almost resting it on the substrate, abdomen maximally raised, a posture characteristic of all Tetrastichinae (see p. 206). Genital contact during less than one second. Short sequences of post-copulatory courtship were observed in *T. evonymellae*.

f. *Tetrastichus*, group *fulvipes*; species observed: *T. calamarius* (fig. 7).

High and low phases alternate distinctly. The low-phase position of the male is very extreme; his high-phase position is mainly due to stretching of the middle legs, the front legs are frequently taken off the female. Duration of low phase about 2 seconds.

Male front tarsi are placed on the female's head. During the high phase the female's antennae point to front, male antennae are raised sideways and to front.

At the onset of the low phase the male bends far over the female's head, drumming his front tarsi on her eyes, his antennae touching or drumming on her mouth parts, his mouth parts very near her mouth parts and his wings vibrating. Male antennal movements are very simple. The female's antennae are folded in front of head during the low phase. Males may perform a kind of stepping movements with their hind legs on the female's wing edges during the low phase.

Female receptivity occurs at end of antennal drumming. Genital contact lasts about 30 seconds. There was always some post-copulatory display. A female may signal renewed receptivity, and, if so, another copulation will follow before the male walks off.

g. *Tetrastichus*, group *lycidas*; species observed: *T. abydenus, T. pallipes, T. strobilanae, T.* spec. 5, *T.* spec. 6 (fig. 8).

In general the alternation of high and low phases is rather distinct. Low phase usually of short duration, high phase longer and more variable.

Male front tarsi are placed on the female's

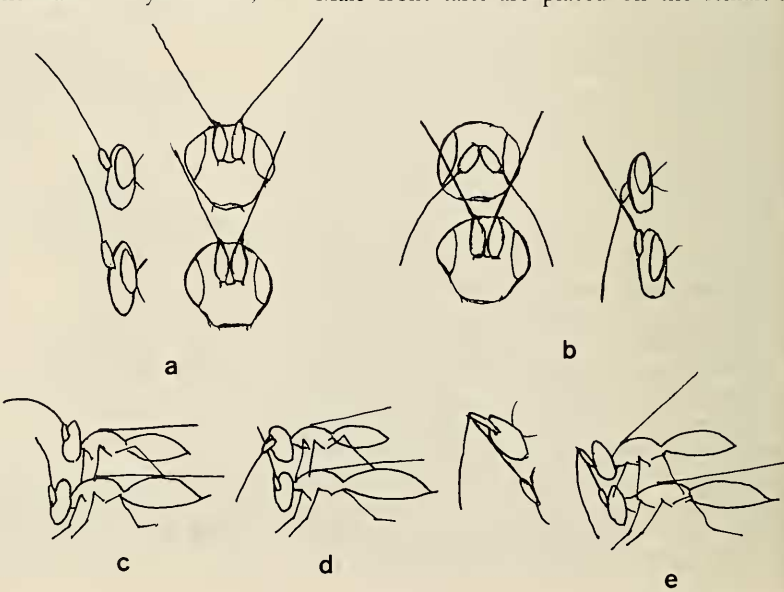


Fig. 8. *T. lycidas* group; a, and c, positions during high phase; b, and d, positions during low phase; e, low phase positions of *T.* spec. 6.

"shoulders". Female antennae point upwards throughout. The position of the male's antennae seems to vary between species. (Upwards in *pallipes*, curved to front in *abydenus*, spread sideways in *strobilanae*, fig. 8a.)

At the beginning of a low phase the male vibrates his wings and brings his mouth parts near the female's pedicel, sometimes pressing his face against her flagella. His antennae are lowered and spread sideways to the front. At the same time he starts series of head-shaking movements which bring his antennae in alternate contact

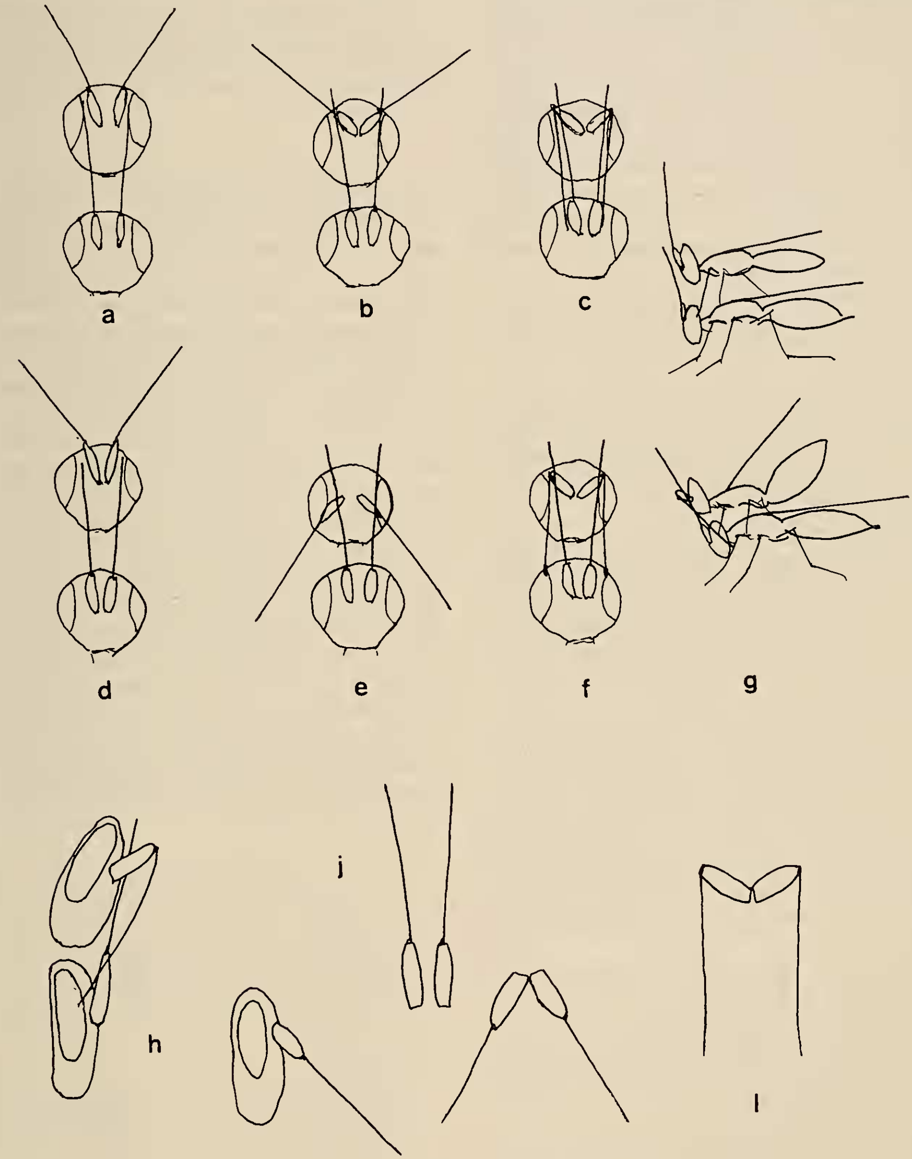


Fig. 9. *T. miser* group; a—c, *T. asparagi* c.s.; d—l, *T. atriclavus*; a, and d, positions during high phase; b, c, e, f, idem during low phase; g, ♂ and ♀ *T. atriclavus* in high, resp. low phase position in sideview; h, male and female heads and antennae during drumming; j—l, male antennal postures in sequential order; j is the initial posture, adopted during the high phase, i, is similar to k, but seen from aside, l is the drumming posture, seen from front.

with the female's antennae from the outside, at the same time rubbing his face against her flagellar parts. Females were not receptive.

The display of *T.* spec. 6 differed in some points and seems to be of considerable interest (see p. 217). High- and low-phase positions of the male were more distinctly different than in the other species. Male front tarsi were placed on the female's head. Male antennae were curved to front during high phase. Instead of head shakes, the male performed rocking movements with the entire body during the low phase: the tip of his abdomen remained stationary, his frontal parts swayed from side to side, wings vibrating. Male antennae seemed to "grasp" the female's antennae at the ipsolateral side during these rocking episodes.

h. *Tetrastichus*, group *miser*; species observed: *T. asparagi*, *T. atriclavus*, *T. hylotomarum*, *T.* spec. 12 (fig. 9).

In general there is a distinct alternation of high and low phases. The duration of the high phase is variable, but in *atriclavus* durations are fixed and both high and low phase are of an equally short duration.

Male front tarsi are placed on the female's "shoulders" (*asparagi*, spec. 12, *hylotomarum*), or on her head (*atriclavus*, presumably also in *incertus*, fide Miller, 1966). Female antennae point upwards throughout, forming a sharp figure V. Male antennae in a similar posture during the high phase only (fig. 9a, d).

The low phase starts with the male bending forward to some extent, vibrating his wings. A sequence of antennal movements follows: antennae are spread sideways (fig. 9b, e) and kept in this position for a moment, then bent and drummed on the female's head in bouts of very rapid movements (fig. 9c, f). The male abdomen is raised very conspicuously, especially during the low phase.

Female receptivity occurs during antennal drumming. Genital contact one second or less. No post-copulatory courtship.

Females of *T. atriclavus* were observed to head-shake during the low phase as long as they remained unreceptive.

i. *Tetrastichus clavicornis*, *species sola*.

There is a distinct alternation of high and low phases.

Male front tarsi are placed on the female's "shoulders". Female antennae point to the front, male antennae are raised, pointing high and to the front.

At the beginning of a low phase the male lowers his body, vibrating his wings. His mouth parts come near the female's pedicels, his antennae are bent, vibrating outside the female's antennae; there are no additional antennal movements.

Only incomplete sequences of courtship were observed, females were very unreceptive. The observed position of the female's antennae may not be the normal position for females engaged in courtship.

Displays of other Tetrastichinae

a. Courtship of *Crataepus marbis* (fig. 10).

Crataepus marbis reminds one of mole-crickets, its external morphology being probably an adaptation to moving through the dense pilosity of the natural habitat (composite flower heads). In *Crataepus* there is an extreme difference between positions in low and high phase. High and low phases alternate very fast but they do not seem to be completely rigid.

Male front tarsi are placed on the female's head, front legs are stretched, antennae are curved above female's.

At the onset of a low phase the male bends his front legs, brings his mouth parts in contact with the female's pedicels and folds his antennae against the female's antennae from the outside. The tips of his flagellae are pressed against the female's mouth parts. Male antennae are neither spread nor raised. There are no wing vibrations nor other movements with legs. Females receptive at the end of a low phase; the female's head is only slightly forward in the copulation posture, her antennae point upwards. Genital contact about 15 seconds.

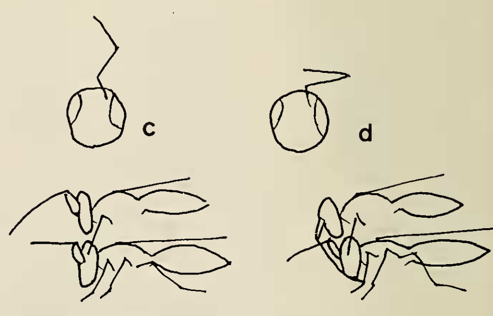


Fig. 10. *Crataepus marbis*; a, high phase, and b, low phase positions; c, and d, female head from front with a male's front leg on top (stretched during high, bent during low phase).

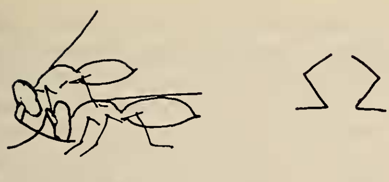


Fig. 11. *Nesolynx albiclavus*; a, low phase position; b, posture of male's middle legs during the drumming episodes.

b. Courtship of *Nesolynx albiclavus* (fig. 11).

The male assumes a low-phase position following mounting and the relative position of male and female heads does not change during the display.

Male front tarsi are placed on female's face near her scapi. The male raises his antennae, spreading them slightly, and flutters his wings at the same time. Then his antennae are spread further and folded over the female's antennae in such a way that her antennae are pinched in between his flagellar parts. Males clearly search for a hold of female antennae before proceeding with the embrace. At the end of a pinching episode the male starts drumming his middle legs on the female's thorax with high frequency. Synchronously he drums on her dorsum with the tip of his abdomen which is bent down. During drumming male antennae rub up and down against female antennae.

Onset of female receptivity is at the end of an antennal embrace; females apparently need relatively long bouts of courtship to become receptive. Genital contact 1—2 seconds. No post-copulatory display.

c. Courtship of *Melittobia acasta* (fig. 12).

Melittobia species exhibit strong sexual dimorphism. Males bear peculiarly shaped antennae with inflated scapes which play an important role in courtship. *Melittobia acasta* is the only European species. Comparative work on this genus will be published in a separate paper.

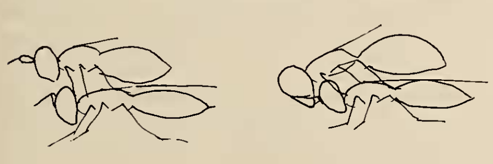


Fig. 12. *Melittobia acasta*; a, high phase, and b, low phase positions in sideview.

Male front tarsi are placed on the female's neck, the male grasps the flagellar parts of the female and holds them in the concave distal area of his scapes. A high phase follows immediately: male loosens his grip, lets female antennae go, spreads and raises his antennae, stretching front legs to some extent, and performs swaying movements with his hind legs, more or less synchronously, up and down the female's thorax. Then, the male bends forward again, grasps the female's antennae which were kept more or less folded in front of her head, and starts quivering his flagellae. At the end of a quivering series the male claval parts touch the female's mouth parts. Quivering is concluded by a distinct pinch by the pedicel and scape as the male flagella and scape are drawn together. Contact between antennae is broken off again. The next high phase, with hind leg movements etc., follows.

In the course of the display antennal contact becomes permanent and the male no longer takes up the high-phase position although the rhythmic sequence of antennal and hind leg movements goes on. Alternations occur more and more rapidly until the movements almost overlap. At this point the male's finale sets in: coordination of hind leg movements changes conspicuously, they are rubbed against the female thorax, for a few seconds, like riding a bicycle. The hind legs are placed on the female again and now middle legs are taken off the female and moved far to the front (as far as the female's head or even beyond) and back again. It is only here that a female *Melittobia acasta* may indicate sexual receptivity. There are no exceptions to this rule. The display of *Melittobia* differs from all the other Tetrastichinae in this important aspect: a sequence is not simply a repetition of similar elements but is built up in time, with new elements being added during the display.

A number of *Melittobia* species (e.g., members of the *hawaiiensis*-complex) do not alternate between high and low-phase episodes but relative position of heads remains about constant from the beginning and antennal contact is permanent throughout (Dahms, 1973). *Melittobia* sequences last much longer than those of other species (in *M. acasta* they are relatively short, in the order of 1—5 minutes, in *M. australica* may be up to half an hour!). Genital contact during about 7 seconds. There is no post-copulatory courtship.

COMPARISONS AND DISCUSSION

Similarities between species groups

The species that were available for study belong to four genera: *Tetrastichus* Haliday, 1844; *Crataepus* Förster, 1878; *Nesolynx* Ashmead, 1905 and *Melittobia* Westwood, 1847. *Tetrastichus* species represent eight species groups and one *species sola*. All species are enumerated in the Appendix.

If we consider entire displays, our species fall into two different categories. The first category accommodates those species whose males perform a more or less elaborate antennal display including relatively long contacts with the female's antennae. Often it involves embraces: either the male grasps the female's antennae with his own and holds them, or he pushes them together in between his, while he bends forward over her head, sometimes touching her mouth parts with his clava or even with his mandibular palpi. In this category are placed *Crataepus marbis*, *Nesolynx albiclavus*, *Melittobia* species, the *Tetrastichus arundinis* group and *Tetrastichus calamarius*.[1])

Our second category accommodates the remaining species groups of *Tetrastichus*, whose males neither hold the female's antennae for some time in some sort of embrace nor bend forward over the female's head. This second category is not uniform, two or three clusters of species groups can be distinguished. The general nature of male display in this category is suggestive of some kind of dichotomy. In one branch, with the species groups *lycidas* and *caudatus*, males exhibit distinct sideways tendencies in the low phase of courtship, rocking the entire body from side to side as in *caudatus* species or in *lycidas* species 6, or shaking the head, as in the other species of the *lycidas* group. In the other branch, with the species groups *evonymellae*, *miser* and *brevinervis*, the general direction of movements is parallel to the length axis of the body. The position of the *daira* group is not clear (see below).

The courtship display of the two observed *evonymellae* group species is rather simple: alternation of distinct high and low phases, and in the low phase a simple antennal display alongside the female's antennae. To some extent it resembles the displays of those males of the *miser* group which court from a position on the female's thorax ("shoulders") but in those males the antennae perform series of knocking movements, hitting the female's head, while the male's abdomen is raised conspicuously during the display. Courtship in the *brevinervis* group, with only one species observed, however, is like a simplified version of *evonymellae* or *miser*. There are no up and down movements with the antennae, but only one upward stroke following low posturing. The posture of the male's abdomen suggests an affinity with *miser*. Males of the *daira* group exhibit sideways tendencies which seem to point to the *lycidas-caudatus* branch and *caudatus* males quiver the antennae in front of the female in a *daira*-like fashion but there is some ambiguity with the display of *T. daira* itself. It was the only *daira* group species observed with the male courting on the female's thorax, and it exhibits elements in its display which are suggestive of the *miser* group, e.g., the female antennae point upward and the male performs series of knocking movements with his antennae, hitting the female's head. The more frontally courting *daira* group males exhibit a more or less similar feature, but instead of hitting the female's head hit, her antennae from the outside.

Our two categories do not cover entirely the currently accepted division, i.e., the genus *Tetrastichus* versus the other genera of Tetrastichinae. Judged by behavioural criteria some species of *Tetrastichus* belong to our first category (i.e. the species of the *arundinis* group, and *T. calamarius*). There are some morphological features which also point this way. The *fulvipes* group may have affinities to *Melittobia* Westw. For example, the inflated scapes of males of some species suggest such relation. *T. calamarius* has a peculiar, flattened habitus which is very suggestive of *Melittobia* species, as does the male's position during courtship. Most species of the *arundinis* group can be distinguished from the other groups of *Tetrastichus* but morphological criteria were insufficient to separate them all. With the addition of behavioural criteria as we now know them, we would suggest to move this species group, and *T. calamarius* (and perhaps the entire *fulvipes* group) out of *Tetrastichus* s.s.

Some kind of dichotomy in our second cat-

[1]) Although *T. calamarius* is currently placed with the *fulvipes* group, it seems to be an aberrant species which may deserve the status of a separate genus; if it actually belongs to the *fulvipes* group, it is a highly specialized species (Graham, pers. comm.). For this reason we do not take it to represent the entire *fulvipes* group.

egory is also indicated on morphological criteria. The groups *miser* and *brevinervis* are characterized by having only one single bristle on the subcostal vein of the fore wings (and as such constituted the former genus *Tetrastichus*). The groups *evonymellae* and *daira* (and some others) have the pygostylar setae of nearly equal length; the groups *lycidas* and *caudatus* (and some others) have one bristle far longer than the others. These two clusters have been recognized as separate species groups by Graham (1961) and Domenichini (1965). Whether or not one or more of these clusters are to be regarded as separate genera or subgenera is not a question to be settled on our present evidence. More could be said, no doubt, with more observations on a greater variety of species.

Our conclusion on the available evidence is that within species groups, species have many features of their courtship display in common. Some groups are much more similar to each other than other groups. Further, there seems to be a parallel to similarities and differences of certain morphological features, features believed to be unrelated to courtship movements.

Evolution of patterns of courtship behaviour in the Tetrastichinae

In the preceding section we have pointed out differences and conformities: certain groups resemble each other much more than others. However, mere resemblances do not guarantee a close relationship. In this section we are going to make a few suggestions on relationships between groups judged by shared characteristics which are to be understood as modifications of more original conditions. Groups not showing such modifications would qualify as being more primitive in that respect, i.e., having retained a more original condition.

Of course, our observations cover only a minute fraction of the Tetrastichinae known to exist. Therefore, we present our data for what they are worth. However, we believe that our data indicate several transformations from more original to more modified situations which have occurred in the evolutionary history of courtship of Tetrastichinae.

The performances of category I males are of a considerable complexity and it seems very difficult to label them as original because of this complexity. They rather appear to represent modifications; most obviously this is true for those species where holding the female's antennae for long periods goes together with the presence of peculiar morphological structures serving such a function, e.g., *Melittobia*, where the male antennae turn out to be effective claspers. Males of all species which practise clasping or embracing or contacting the female's mouthparts, court from a frontal position, i.e., on the female's head or neck. In these species the female holds her antennae in a forward position or she folds them in front of her head.

Neither frontal position of the male nor a forward position of the female's antennae are tied to grasping or embracing (e.g., several species of the group *daira*, or *T. lasiocera* group *brevinervis*). Placement of the male's fore tarsi and position of the female's antennae seem to be independent to some degree but two combinations occurred most frequently: tarsi on head/antennae forward or folded, and tarsi on "shoulders"/antennae upright. The first combination is most likely to represent a derived condition, as we pointed out above. It follows, on the assumption that both categories are genuinely related, that the second combination qualifies as a more original condition. The alternative possibility of being another specialisation is unlikely: an upright position of female antennae during courtship appears to be a widespread phenomenon, occurring in diverse groups. Moreover, we also observed it in Elachertinae, a group of Eulophidae believed to be near the origin of Tetrastichinae. The postures of female antennae are illustrated in fig. 13.

It should be noted that we found the female's antennal posture to vary within one group (*dai-*

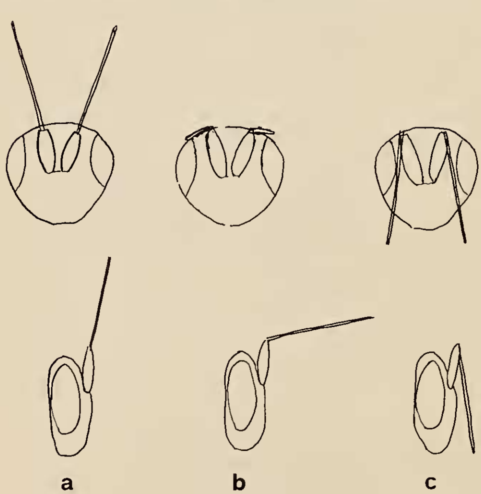


Fig. 13. Female antennal posture during low phase in different groups. Further explanations in the text.

ra) and the placement of the male's fore tarsi in at least three (*lycidas*, *daira*, *miser*). There are no good reasons for splitting these groups on this basis as we feel transitions have occurred in separate groups independently a number of times.

A frontal placement of the male seems to be derived from a more caudally located placement. Earlier we have reached this conclusion with Pteromalidae where the original position for courting is the same as the position for mating. Based upon Van den Assem (1976), we have arguments to assume that in this group the switch of courtship position of the male from the rear to the front, the development of an antennal receptivity signal by the female, and the reduction of male size constitute a complex of derived characters. In Eulophidae a parallel development seems to have taken place although we did not find truly caudal courters. An interesting point in this respect is that the antennal posture indicative of sexual receptivity of female Tetrastichinae is the reverse of the antennal signal of Pteromalinae, i.e., antennae stretched and upright in Tetrastichinae versus antennae bent down and drawn to the head in Pteromalinae. Reduction of male size is a common phenomenon in many Chalcidoidea including Tetrastichinae. Within the Tetrastichinae *Melittobia* are a notable exception. However, taking account of the reproductive strategy of *Melittobia*, this exception is at once clear enough (Van den Assem, Gijswijt & Nübel, 1980).

A few additional evolutionary changes may be pointed out (see table 1 for a summary of our ideas). In many species or species groups there is a regular alternation of low and high-phase episodes, in others there is not. Species of our category I may serve as example of this latter condition. In some category I species a regular alternation occurred (*Crataepus marbis*, *Tetrastichus calamarius*, species of the *arundinis* group), in some alternations were only observed in the first part of a sequence of courtship, the high phase being dropped later (several species of *Melittobia*) whilst in some there never was a true alternation at all, males being continuously in a low-phase position (*Nesolynx albiclavus*, several species of *Melittobia*). In contrast, most of the category II males exhibited distinct alternation of high and low-phase episodes over the entire sequence of courtship. We believe that absence loss of high-phase episodes can be understood as a derived condition.

Another development has to do with the timing of alternations. In some species the durations of high and low phases vary, most often the high phases have no fixed duration (e.g., *Tetrastichus* spec. 9), in others the timing of alter-

Table 1. Evolutionary modifications of courtship behaviour of Tetrastichinae.

More original condition	derived condition
alternation of high and low phases	high phases dropped underway high phases never occur
alternation between more caudal and more frontal positions of ♂ only slight	alternation between more caudal and more frontal positions of ♂ far more extreme
timing of alternations variable	timing of alternations stereotyped
patterns of ♂ antennation as rubbing or lashing ♀ antennae or head	♂ embraces ♀ antennae ♂ antennae (claval parts) make contact with ♀ mouth parts
♀ antennae pointing upwards	♀ antennae pointing to the front ♀ antennae folded in front of head
♂ front tarsi on ♀ thorax	♂ front tarsi on ♀ neck ♂ front tarsi on ♀ head
display without leg movements	display includes ritualized leg movements
♂ display a repetition of similar elements	new elements come in underway
events tied to female's sexual receptivity occur at intervals	female receptivity occurs at only one single point of the male's display

nations has become completely rigid (e.g., *T. atriclavus, T. arundinis*). The latter condition is most probably to be understood as a derived one: development towards a high degree of stereotypy is found in many groups, in fact it appears to be a very general phenomenon.

Yet another development applies to the onset of female sexual receptivity. Usually only virgin females will respond to courtship by a conspecific male. In those species where the male's display is a repetition of similar elements, female receptivity usually sets in at fixed points (e.g., at the end of an antennal lashing series in *T. daira*; at the end of an antennal embrace in *Nesolynx*). In *Melittobia* (except for the most primitive species, Van den Assem et al., in prep.) female receptivity occurs at only one single point in time which is immediately following the male's "finale" performance (Van den Assem, 1975).

Lastly we draw attention to leg movements as part of the courtship ritual. Movements of many types with any pair of legs may be performed, e.g., there are drumming the fore legs on the female's head or eyes, hammering middle legs on the female's thoracic pleura and swaying middle or hind legs back and forth, sometimes reaching the female's head or beyond. Bristles of many kinds are placed on all parts of legs and they may provide an array of stimuli to different parts. Leg movements of some kind are included in displays of almost all category I males whereas they appear to be very rare in the category II group; *T. epicharmus* is such a rarity. Most probably leg movements constitute later modifications of the courtship ritual in the Tetrastichinae.

Above we have pointed out a number of transitions which we believe to have taken place in the evolutionary history of the Tetrastichinae. Our ideas on this point are summarized in table 1. Many of the characters which we understand as modifications occur in the displays of category I males. As these characters are shared by the whole group, they render it a certain cohesion which seems to point to common ancestry. Such a cohesion does not seem to exist in category II. Perhaps the groups included here are not closely related, although they share several features. These features which include the following, are likely to be of a more primitive character than those of category I: male courtship position more to the rear (his front tarsi placed on the female's thorax); distinct alternation of high and low phases, and duration of high phase episodes variable; female's antennae upright throughout the male's display, male's antennae upright in the high phase and moving up and down along the female's antennae in the low phase; male tarsi remain in a fixed position throughout. According to our views the group *evonymellae* yields a picture of a rather generalized, original pattern of tetrastichine courtship behaviour.

Domenichini (1965) placed the group *strobilanae* (= *lycidas* + *caudatus*) at the base of his reconstruction of the phylogeny of the *Tetrastichus* complex because of what he called its morphologically non-specialized nature. Courtship characteristics of this group do not seem to support such a conclusion without reservations, but they do seem to support another. Domenichini derived, among others, the groups *viridimaculatus* (= *arundinis*) and *fulvipes* from its branches. It is worth mentioning that some similar conclusion might be drawn from a comparison of courtship patterns (with many reservations!). *T.* spec. 6 (group *lycidas*) males perform antennal movements which resemble grasping movements to some extent; *T. dotus* (group *caudatus*) males align their antennae along the female's for a moment and the female's claval parts align the (somewhat inflated) scapi of the male. Both these displays are suggestive of incipient stages of behaviour patterns of category I displays.

As has been stated above, our observations cover a limited number of species. Moreover, our sample appears to be heavily biased: the majority of our species are parasitic on gall midges. As a rule, such a state of affairs is highly unfortunate but apparently it is not for a comparative study of courtship behaviour. Other kinds of behaviour (e.g., parasitisation behaviour) are much more prone to host influences. No doubt this is the reason why Domenichini was unable to find such separating features when he tried to find behavioural characteristics for separating *Tetrastichus* species-groups and based his observations on parasitisation behaviour and preferences for certain types of hosts. He came across a number of very striking convergencies in species from different groups parasitising similar host species. Our observations confirm that patterns of courtship behaviour are highly independent of host characteristics, a result which did not surprise us.

Male courtship displays have presumably evolved as the (to the males) most effective way to overcome female "coyness". It has led to the production of highly specific stimuli. Taxonomists can be helped considerably when trying to

solve classificatory riddles by taking notice of the insects' own advertisements, especially in cases of clusters of sympatric, sibling species, which is commonplace in Chalcidoidea. There can be no doubt about the role which behavioural characters (courtship characteristics in particular) are going to play in future taxonomic work. We have results which indicate that ethological, isolating mechanisms (e.g., sex pheromones) may be already fully effective before entities can be separated on morphological features. In a forthcoming paper on *Melittobia* we will return to this point and provide a few examples. If such a situation would turn out to be a general phenomenon in parasitic Hymenoptera — and we believe it will — behaviour studies will even become indispensable. For the time being there can be no doubt about the value of behavioural characters as supplementary to morphological data.

ACKNOWLEDGEMENTS

A number of colleagues sent us living specimens for our observations. Their help is greatly appreciated. All material received has been listed in the Appendix. We are greatly indebted to Dr M. W. R. de V. Graham (Oxford) for identifications and for discussions, both at Leiden and Oxford. Drs Graham and E. C. Dahms (Brisbane) commented on a manuscript draft of the paper and helped to improve the final version. The investigations were supported by the Foundation for Fundamental Biological Research (BION), which is subsidized by the Netherlands Organisation for the Advancement of Pure Research (ZWO).

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APPENDIX

LIST OF SPECIES MENTIONED IN THE TEXT AND ORIGIN OF OUR MATERIAL

Species marked (*) have been observed in courtship. Material has been deposited in the collections of M. J. Gijswijt (G) and Institute for Taxonomic Zoology, Univ. of Amsterdam, The Netherlands (ITZA).

* *Tetrastichus abydenus* (Walker), group *lycidas*; from galls of *Rhabdophaga terminalis* (Dipt.) on *Salix* sp., Voorschoten, The Netherlands, viii.1978, 7♂ 10♀ (G, ITZA).

* *Tetrastichus arundinis* Giraud, group *arundinis*; from puparia of Diptera on *Phragmitis australis*, Kroonpolders, Vlieland, The Netherlands, iii.1977, coll. J. H. Mook, fair numbers (ITZA).

* *Tetrastichus asparagi* Crawford, group *miser*; from eggs and larvae of *Crioceris asparagi* (Col.) on *Asparagus officinalis*, Meijendel, Wassenaar, The Netherlands, vi.1975, ix.1978, coll. J. van Alphen, 10♂ 16♀ (G, ITZA). Geysteren, The Netherlands, vii.1976, 1♂ 4♀ (G).

* *Tetrastichus atriclavus* Waterston, group *miser*; from pupae of *Acigona ignefusalis* (Lep.), via IRAT, Montpellier, France, from Sénégal, West Africa, xii.1978, leg. J. Brenière, several hundreds, sex ratio 1♂ : 3♀ (G, ITZA).

Tetrastichus brevicornis (Panzer), group *brevicornis*; from seed pods of *Sarothamnus scoparius*, Bentheim, Westph., Germany, iv.1977; Beilen, The Netherlands, ix.1977, 2♀ (G).

* *Tetrastichus calamarius* (Graham), group *fulvipes*; from galls of *Giraudiella inclusa* (Dipt.) on *Phragmitis australis*, Leiden, The Netherlands, ii.1974, Kroonpolders, Vlieland, The Netherlands, iv.1977, coll. J. H. Mook, large numbers, many more females than males (G, ITZA).

* *Tetrastichus clavicornis* (Zetterstedt), *species sola*; from catkins with *Semudobia* spp. (Dipt.) on *Betula* sp., Meijendel, Wassenaar, The Netherlands, iii.1978, 22♂ 36♀; Oberstdorf, Allg., Germany, xii.1977, 8♂ 6♀ (G).

* *Tetrastichus daira* (Walker), group *daira*; from flower heads of *Cynara cardunculus*, Ronda, Andalusia, Spain, ix.1978, 110 specimens, 10—20% ♂ (ITZA).

* *Tetrastichus diaphantus* (Walker), group *daira*; from galls of *Biorhiza pallida* (Hym.) on *Quercus pubescens*, M. Ventoux, Dep. Vaucluse, France, vii.1978, 16♂ 60♀ (G, ITZA).

* *Tetrastichus dotus* (Walker), group *caudatus*; from galls of *Dasineura ulmariae* (Dipt.) on *Filipendula ulmaria*, Voorschoten, The Netherlands, vii.1976, v.1980, 3♂ 15♀ (G, ITZA).

Tetrastichus ecus (Walker), group *ecus*; from leaf mine of *Phyllonorycter* sp. (Lep.) on *Fagus sylvaticus*, Hortus Botanicus Leiden, The Netherlands, x.1976, 3♀.

* *Tetrastichus epicharmus* (Walker), group *caudatus*; from seeds of *Papaver dubium*, St. Auban s. Ouvèze, Dep. Drôme, France, viii.1978, 14♂ 11♀ (G, ITZA).

Tetrastichus eriophyes Taylor, group *lycidas*; from galls of *Phytoptus avellanae* (Acar.) on *Corylus avellana*, Brochterbeck, Westph., Germany, v.1976, thelytokous (G).

Tetrastichus escherichi (Szelényi), group *lycidas*; from catkins with *Semudobia* spp. (Dipt.) on *Betula* sp., Meijendel, Wassenaar, The Netherlands, v.1976, 1♀ (G).

* *Tetrastichus evonymellae* (Bouché), group *evonymellae*; from pupae of *Yponomeuta padellus* (Lep.) on *Crataegus monogyna*, Vogelenzang, The Netherlands, vii.1974; on *Prunus padus*, Leiden, The Netherlands, vi.1976, coll. J. de Groot, fair numbers.

* *Tetrastichus galactopus* (Ratzeburg), group *evonymellae*; hyperparasite of a braconid in a caterpillar of *Pieris brassicae*, Wageningen, The Netherlands, ix.1973, leg. K. W. R. Zwart, fair numbers (G).

* *Tetrastichus gratus* Giraud, group *arundinis*; from puparia of Diptera on *Phragmitis australis*, Kroonpolders, Vlieland, The Netherlands, iii.1977, coll. J. H. Mook, fair numbers (G).

* *Tetrastichus hylotomarum* (Bouché), group *miser*, from pupae of *Arche rosae* (Hym.) on *Rosa* sp. (cultivar), Schoonebeek, The Netherlands, ix.1976, coll. A. van Frankenhuyzen, 14♂ 19♀ (G).

* *Tetrastichus lasiocera* Graham, group *brevinervis*; from galls of *Perrisia persicariae* (Dipt.) on *Polygonum amphibium*, Oegstgeest, The Netherlands, x.1978, 2♂ 9♀ (G).

Tetrastichus legionarius Giraud, group *miser*; from puparia of *Lipara lucens* (Dipt.) on *Phragmitis australis*, Oostelijk Flevoland, The Netherlands, vi.1978, coll. J. H. Mook; 34 specimens.

Tetrastichus lycidas (Walker), group *lycidas*; from galls of *Hartigiola annulipes* (Dipt.) on *Fagus sylvatica*, 's-Graveland, The Netherlands, ix.1977; 2♂ 2♀ (G).

Tetrastichus lysippe (Walker), *species sola*; from galls of *Dasineura crataegi* (Dipt.) on *Crataegus monogyna*, 's-Graveland, The Netherlands, vii.1976, 3♂ 20♀ (G).

* *Tetrastichus pallipes* (Dalman), group *lycidas*; from

galls of *Semudobia* sp. (Dipt.) on *Betula* sp., Meijendel, Wassenaar, The Netherlands, v.1976, few specimens; Oberstdorf, Allg., Germany, ix.1977, 1♂ 3♀ (G).

Tetrastichus spartii (Ratzeburg), group *lycidas*; from seed pods of *Sarothamnus scoparius*, Bentheim, Westph., Germany, iv.1977, 1♀ (G).

Tetrastichus strobilanae (Ratzeburg), group *lycidas*; from cones of *Picea abies*, Oberstdorf, Allg., Germany, i.1977, xii.1978, 3♂ 2♀; 3♂ 5♀ (G).

The following species of *Tetrastichus* are new species which will be described by Dr. M. W. R. de Vere Graham (Oxford).

Tetrastichus spec. 1, group *brevinervis*; from seed pods of *Papaver dubium*, Entrechaud, Dep. Vaucluse, France, vii.1978, 10♀.

Tetrastichus spec. 2, group *caudatus*; on *Verbascum* sp., Serrania de Ronda, Andalusia, Spain, ix.1978, 2♀.

* *Tetrastichus* spec. 3, group *daira*; from seed pods *Papaver dubium*, Dep. Vaucluse, France, summer 1975.

* *Tetrastichus* spec. 4, group *daira*; from flowerheads of *Centaurea* sp., Oberstdorf, Allg., Germany, xii.1977, 9♂ 38♀.

* *Tetrastichus* spec. 5, group *lycidas*; from *Foeniculum vulgare*, Carratraca, Andalusia, Spain, ix.1978, 2♂ 4♀.

* *Tetrastichus* spec. 6, group *lycidas*; from galls of *Plagiotrochus* sp. on *Quercus ilex*, Alhaurin de la Torre, Andalusia, Spain, iii.1979, 1♂ 1♀.

Tetrastichus spec. 7, group *lycidas*; from gall on top of twigs on *Salix* sp., St. Auban s. Ouvèze, Dep. Drôme, France, vii.1978, 1♀.

Tetrastichus spec. 8[1]), group *lycidas*; from galls of *Dasyneura epilobii* (Dipt.) on *Chamaemerion angustifolium*, Voorschoten, The Netherlands, viii.1978, few specimens.

* *Tetrastichus* spec. 9, group *arundinis*; from *Phragmitis australis*, Kroonpolders, Vlieland, The Netherlands, iii.1977, coll. J. H. Mook, few specimens.

Tetrastichus spec. 10, group ?; from galls of *Rhodites spinosissimae* on *Rosa pimpinellifolia*, Bloemendaal, The Netherlands, ix.1977, 1♂ 11♀.

* *Tetrastichus* spec. 11[1]), group ?; from galls of *Dasineura epilobii* on *Chamaenerion angustifolium*, 's-Graveland, The Netherlands, viii.1976, 1♂ 26♀.

* *Tetrastichus* spec. 12, group *miser*; from eggs of *Crioceris duodecimpunctata* on *Asparagus officinalis*, Meijendel, Wassenaar, The Netherlands, coll. J. van Alphen, few specimens.

* *Crataepus marbis* (Walker); from flowerheads of *Carduus* sp., Malaucène, Mt. Serain, Dep. Vaucluse, France, viii.1978; idem of *Cynara cardunculus*, Ronda, Andalusia, Spain, ix.1978, numerous specimens, sex ratio ca. 1 : 1.

Hyperteles elongatus (Foerster); from galls of *Mikiola fagi* on *Fagus* sp., Bentheim, Westph., Germany, iv.1977, 1♂ 1♀; Oberstdorf, Allg., Germany, ix.1977, 2♂ 4♀.

Hyperteles luteus (Ratzeburg); from galls of *Mikiola fagi* on *Fagus* sp., Bentheim, Westph., Germany, iii.1977, 2♀.

* *Melittobia acasta* (Walker), parasite of *Odynerus spinipes* (Hym.), Losser, The Netherlands, vi.1974, coll. G. A. Bekke; parasite of *Omalis aureus* (Hym.) and *Ancistrocerus* sp. (Hym.), Ede, The Netherlands, vi.1976, coll. R. Leys; ca. 5% ♂ in lab. cultures.

* *Nesolynx albiclavus* (Kerrich), from puparia of *Glossina* sp. (Dipt.), obtained via Lab. Exp. Entomology Amsterdam, from Salisbury, Rhodesia, leg. G. A. Vale, iv. 1977, very skewed sex ratio.

[1]) *T.* 8 and *T.* 11 may be the same species.